Changes of Some Physiological Characteristics and Agronomic Traits during Genetic Improvement of Soybean Cultivars in Jilin Province of China

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Abstract: Soybean yield in the world increased significantly with year of release. Future yield increase may be dependent on an understanding of the changes in soybean cultivars made by breeding and selection. However, the yield of new soybean cultivars did not show a linear increase in recent years in China. This may be related with that no clear physiological indexes were used for the selection of high yield soybean cultivars. The objective of this paper is to provide a review on some physiological characteristics changes associated with yield increase during the genetic improvement of soybean from 1923 to 2005 in Jilin province. At the same time, in order to evaluate the changes of physiological characteristics, a comparison between some physiological characteristics and some agronomic traits was made. We found that the genetic improvement of agronomic traits by soybean breeding has made obvious progress, meanwhile, some physiological characteristics were improved, while the percentage changes of physiological characteristics were smaller than those of agronomic traits. The genetic improvement of some physiological characteristics, such as, photosynthetic ability, apparent mesophyll conductance (ALMC), nitrate reductase activity (NRA), the number of nodule still have huge yield potentiality. Soybean breeding with physiological characteristics as breeding targets will have big improvement in soybean yield.

Key words: Soybean; Genetic improvement; Physiological characteristics; Agronomic traits; Seed yield

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吉林省不同年代育成大豆品种某些农艺性状和生理性状的比较

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摘 要:许多研究表明,世界大豆品种产量随着育成年代呈显著增加,但自20世纪90年代以来我国育成大豆品种的产量增加幅度有放缓和停止不前的变化趋势。说明以农艺性状为选择目标的常规育种其品种的产量潜力已受到限制。迫切需要建立新的育种目标和计划。大豆育种工作者在对大豆品种产量和农艺性状进行定向改良时,并没有考虑生理性状的改良,也不清楚生理性状发生了哪些变化。许多研究表明,大豆品种遗传改良过程中其生理性状也发生了变化,并与产量呈密切相关。对1923年至2005年间育成的40个大豆品种农艺性状和生理性状的研究表明,生理性状与产量和农艺性状相比,其改善的幅度较小,说明大豆生理性状的遗传改良孕育着巨大的产量潜力。建立以生理性状为目标的育种程序,定向改变大豆的生物学和生理学特性,是提升当前我国大豆育种水平,实现产量突破的重要途径。总结作者及课题组成员近几年来对吉林省1923年以来育成的大豆品种农艺性状和生理性状的比较研究结果,认为大豆叶片的光合能力、表观叶肉导度、硝酸还原酶活性和根瘤的数量具有作为高产品种选择指标的价值,有待于对其进行选择成本、可靠性、关联性和可替代性进行研究,用于高产大豆品种的选育和改良计划。

关键词: 大豆;遗传改良;生理性状;农艺特性;种子产量

World soybean production has increased sharply in past decades [1-3]. The yield increase based on per unit area was mainly contributed by cultural practices and genetic improvement of soybean cultivars. How to estimate the contribution of genetic improvement, Cox et al [4] pointed out the comparison of cultivars in com-

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mon environments was the most direct estimate of genetic progress. According to the method of Cox et al, many researches showed that yield of soybean cultivars was increased linearly with years of release [5-6] under same cultural and management environment. At the same time, agronomic characteristics[7-8], growth features[9-10] and physiological traits[11-16] were compared to examine the reason of cultivars difference in soybean yield. Specht et al [1] and Ustun et al[8] suggested that soybean yield increase was linear in past several decenniums, this linear increase demonstrate that a yield plateau has not been reached. But, the yield of new soybean cultivars not showed linear increase in recent years in China [3]. This may be related with that no new breeding selection indexes and target are used for the programme of high yield soybean cultivars [3,12,15]. Although many agronomic traits and physiological characteristics were correlated with yield, what target would be used as new soybean cultivars breeding were not determined. The future yield increase may be dependent on an understanding of agronomic traits and physiological characteristics of high yield soybean cultivars by breeders. In order to understand the yield potential of selection indexes of new cultivars in future soybean breeding, forty soybean cultivars released from 1923 to 2005 in Jilin province were grown under the same field conditions, and some agronomic traits and physiological characteristics at R2 and R4 stages were comparative studied simultaneously. The objective of this paper is to provide a review for our research results from 2005 to 2008. We hope that the work will be beneficial to plan further breeding strategic target, and to portend for yield improvement in breeding new high yield soybean cultivars.

1 Materials and methods

1.1 Research location and soybean cultivars

Research work was conducted at experimental station of Jilin Agricultural University, Changchun city, Jilin Province P. R. of China (125.10E Longitude, 43.53N Latitude) in 2005 and 2006. The annual average precipitation is 567mm; ≥10℃ accumulated temperature is 2860℃; annual average temperature is 4.6℃ in Changchun region. Forty soybean cultivars were chosen for research, three most old ancestral soybean cultivars are Huangbaozhu (released in 1923), Yuanbaojin and Mancanjin (both released in 1929), respectively. The latest new cultivars in the experiment are Jinong No. 16 (released in 2005). The time span of release is 82 years (Table 1). Seed was planted on 28 April in 2005 and 29 April in 2006, respectively. The experiment was in a randomized complete block design with three replications. The stand was thinned to 25 plants per m^2 after planting for about three weeks. Cultivars were in five rows of 5 m in length and 0.65 m in width between the rows.

Table 1 Name, year of release, days to maturity and origination in experimental soybean cultivars

Cultivar	Year of release	Days to maturity	Origination
Huangbaozhu	1923	140	JAAS
Mancangjin	1929	135	JAAS
Yuanbaojin	1929	131	JAAS
Jinyuan No. 1	1941	133	JAAS
Jiti No. 5	1956	134	JAAS
Jilin No. 1	1963	140	JAAS
Jilin No. 2	1963	130	JAAS
Jilin No. 3	1963	135	JAAS
Jilin No. 4	1963	135	JAAS
Jilin No. 5	1963	145	JAAS
Jilin No. 6	1963	140	JAAS
Jilin No. 7	1971	125	JAAS
Jilin No. 8	1971	134	JAAS
Jilin No. 9	1971	135	JAAS
Jilin No. 10	1971	128	JAAS
Jilin No. 12	1971	130	JAAS
Jilin No. 15	1978	128	JAAS
Jilin No. 16	1978	142	JAAS
Jilin No. 18	1982	125	JAAS
Jilin No. 20	1984	123	JAAS
Jilin No. 22	1989	116	JAAS
Jilin No. 23	1990	120	JAAS
Jilin No. 26	1991	118	JAAS
Jinong No. 4	1992	128	JLAU
Jilin No. 30	1995	132	JAAS
Jilin No. 35	1995	126	JAAS
Jiunong No. 21	1995	129	JLAC
Jilin No. 36	1996	131	JAAS
Jilin No. 38	1998	135	JAAS
Jilin No. 43	1998	116	JAAS
Jilin No. 47	1999	115	JAAS
Jinong No. 7	1999	129	JLAU
Jilin No. 45	2000	128	JAAS
Jilin No. 55	2001	119	JAAS
Jilin No. 58	2001	115	JAAS
Jinong No. 11	2002	132	JLAU
Jinong No. 12	2002	130	JAAS
Jiyu No. 66	2002	126	JAAS
Jinong No. 15	2004	130	JLAU
Jinong No. 16	2005	132	JLAU

Abbreviations: JAAS – Jilin Academy of Agricultural Sciences; JLAU – Jilin Agricultural University; JLAC – Jilin Agricultural College.

1.2 Method of measurement

Some agronomic traits were measured at R4 and R6 stages. Seed yield was calculated based on per unit area; measurement was made from the three center rows of each plot after 50 cm were discarded in the end of the rows at R8 stage. Physiological characteristics in this paper were measured at R2 and R4 stages, after leaves were collected from plants at 9:00 – 11:30 h, placed in a plastic bag and temporarily stored in a vacuum bottle, where it provide a water saturated and low temperature (4 – 6℃) environment by ice cubes covered with gauze for transport to the laboratory, then the leaves were used for the measurement of physiological characteristics. Volume of nodule, number of nodule and fresh weight of nodule were measured by using 20 soybean cultivars in potted plants.

Net photosynthetic rate and related photosynthetic characteristics were measured with a portable photosynthesis system (model Li – 6400, LI – COR. , Inc. , Lincoln, NE). Measurement works were done at 9:00 – 11:30 with stable red – blue light source under field condition; photo flux density is 1 200 uEm^{-2}·s^{-1}. All the data are means of three days measurement at each growth stage.

2 Results

2.1 Changes of yield and some agronomic traits

There were significant seed yield difference among cultivars, and soybean seed yield increased nearly 1% with the year of release. Days to maturity were decreased significantly with year of release. As the increase of yield and the decrease of days to mature, harvest index and biomass increased with year of release. Plant height and number of branch were decreased; stem diameter was lodging resistance were increased with year of release. Capacity of sink, such as pod number , seed number , and seed weight were increased with the genetic improvement of soybean cultivars. We use leaf area to express photosynthetic production ability of source, and found that although leaflet area was decreased with year of release, node number was increased, and as the result, the number of leaf and leaf area and leaf area index (LAI) were increased. Seed weight per unit leaf area and seed number per unit leaf area were increased with year of release, but, number of blighted pod was increased as the increase of number of pod and seed (Table 2). This result showed the increase of sink capacity was larger than that of source (leaf area).

Table 2 Changes of yield and some agronomic traits during the genetic improvement of soybean cultivars from 1923 to 2005 in Jilin province

Traits	Units	Regression equation	Increase or decrease/%	Correlation coefficient with year of release	Correlation coefficient with yield
Yield	kg·hm^{-2}	$12.541\,0x - 228.34$	80.19	0.82**	–
Maturity	d	$-0.203\,4x + 531.4$	–11.89	–0.53**	–0.25
Harvest index	%	$0.000\,9x - 1.244$	15.16	0.52**	0.55**
Biomass	g·m^{-2}	$1.029\,8x - 1\,624.5$	23.73	0.32	0.36
Number of pod	No.·plant	$0.313\,8x - 562.23$	61.53	0.48*	0.49**
Number of seed	No.·plant^{1}	$0.333\,65x - 616.24$	89.44	0.45*	0.46**
blighted pod	No.·plant^{-1}	$0.033\,7x - 63.929$	315.42	0.55*	0.68**
Seed weight	g·plant^{-1}	$0.120\,7x - 215.48$	59.53	0.72**	0.68**
100 – seeds wt.	g	$0.016\,7x - 17.975$	10.26	0.26	0.19
Plant height	cm	$-0.327\,2x + 753.66$	–21.56	–0.55**	–0.52**
Stem diameter	mm	$0.004\,6x - 8.054\,3$	47.66	0.44*	0.33
Lodging index	–	$-0.025\,4x + 53.011$	–50.00	–0.72**	–0.66**
Number of branch	number	$-0.036\,8x + 75.365$	–65.62	–0.60**	–0.51**
Number of node	number	$0.051\,2x - 80.011$	22.76	0.41*	0.26
Leaf area	plant·cm^{-2}	$0.388\,7x^2 - 1521.6x + 1E + 6$	45.01	0.51**	0.34
Leaflet area	cm^2	$-0.209x + 463.73$	–27.72	–0.37*	–0.37*
LAI	–	$0.006x^2 - 2.213\,8x + 2167.3$	36.03	0.47**	0.49**
Number of leaf	No.·plant^{-1}	$0.002\,6x^2 - 10.027x + 9\,725.8$	151.30	0.58**	0.52**
Seed weight/leaf area	g·dm^{-2}	$0.004\,6x - 8.104\,1$	50.86	0.62**	0.60**
Number of seed/leaf area	No.·dm^{-2}	$0.034\,5x - 61.332$	56.45	0.46*	0.48*

"*" and "**" indicate Significant level at 5% and 1% probability level, respectively

2.2 Changes of some physiological characteristics

Leaf net photosynthetic rate (*Pn*), stomatal conductance (*Gs*), apparent mesophyll conductance (ALMC) and transpiration (*Tr*) were increased significantly with year of release (table,3). As the increase of *Tr* was higher than that of *Pn*, as the result, water usage efficiency (WUE) was decreased with year of release. Specific leaf weight (SLW) and chlorophyll content were increased significantly with the year of release.

Soluble protein content was increased, but it is not shown significant changes with year of release and yield. Leaf soluble sugar content was increased significantly with the year of release and yield. Soybean is a crop of accumulated more nitrogen in seed and absorbed more nitrogen during the growth than other crops. We found that modern cultivars had higher nitrate reductase activity (NRA) in leaf than old cultivars, meanwhile, volume, number and fresh weight of nodule in roots were increased with year of release and yield. Production enzyme activity such as, SOD, POD and CAT in leaf were increased with year of release, but it is not significant. MDA content was increased significantly with year of release and yield.

Table 3 Changes of yield and some physiological characteristics during the genetic improvement of soybean cultivars from 1923 to 2005 in Jilin province

Traits	Units	Regression equation	Increase or decrease/%	Correlation coefficient with year of release	Correlation coefficient with yield
Yield	$kg \cdot hm^{-2}$	$12.541x-228.34$	80.19	0.8161**	–
Pn	$\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$	$0.0469x-68.382$	17.64	0.5760**	0.6102**
Tr	$mmolH_2O \cdot m^{-2} \cdot s^{-1}$	$0.0341x-60.733$	57.76	0.7750**	0.6277**
Gs	$molH_2O \cdot m^{-2} \cdot s^{-1}$	$0.0022x-3.4243$	22.37	0.3278*	0.1613
WUE	$\mu molCO_2 \cdot mmol^{-1} H_2O$	$-0.0123x+27.919$	-23.64	-0.6423**	-0.5166**
Ci	$\mu mol \cdot mol^{-1}$	$-0.2235x+709.6$	-6.55	-0.5705**	-0.2821
ALMC	$mmol \cdot m^{-2} \cdot s^{-1}$	$0.0002x-0.3523$	50.77	0.5254**	0.5211**
Ci/Ca	–	$-0.0006x+1.8005$	-7.61	-0.4446**	-0.3493*
Chl content	$mg \cdot dm^{-2}$	$0.0126x-19.057$	19.97	0.3889*	0.2885
SLW	$mg \cdot dm^{-2}$	$1.1779x-1888.3$	25.63	0.6059**	0.6705**
Soluble protein content	$mg \cdot g^{-1}$	$0.0257x-32.063$	12.14	0.2978	0.1794
Soluble sugar content	$mg \cdot g^{-1}$	$0.0778x-139.24$	61.52	0.5813**	0.4266**
NRA	$\mu g \cdot g^{-1} \cdot h^{-1}$	$1.9531x-3166.9$	27.20	0.7212**	0.6197**
Volume of nodule	$mL \cdot plant^{-1}$	$0.0523x-100.74$	586.92	0.8300**	0.7700**
Number of nodule	$Number \cdot plant^{-1}$	$3.4975x-6665.8$	478.85	0.7200**	0.6600**
Fresh weight of nodule	$g \cdot plant^{-1}$	$0.0533x-102.8$	640.17	0.8400**	0.7800**
SOD activity	$U \cdot g^{-1} FW$	$0.6796x-966.5$	16.37	0.1533	0.1589
POD activity	$OD470/gFW \cdot min^{-1}$	$0.041x-65.622$	25.43	0.2644	0.0472
CAT activity	$U \cdot g \cdot min^{-1}$	$5.7797x-10129$	48.10	0.2316	0.0401
MDA content	$Mmol \cdot g^{-1} FW$	$-0.0573x+127.87$	-26.57	-0.4727**	-0.5355**

3 Discussion

Forty soybean cultivars released from 1923 to 2005 were grown under the same field conditions simultaneously, yield, agronomic traits and physiological characteristics were compared, the results indicated soybean breeder have made great genetic improvement in yield, some agronomic traits and physiological characteristics. The changes of yield and related agronomic traits were the results selected by soybean breeder, Our results of yield and agronomic traits genetic improvement are consistent with the estimate of Wilcox et al.[2] in sixty years of soybean genetic improvement, and is nearly in concordance with the results from Boerma[17], Voldeng et al.[7], Kumudini et al.[9] and Ustun et al.[8]. The increase of yield was correlated with the improvement of agronomic traits, such as biomass, harvest index, lodging resistance, number of pod and seed, days to maturity, plant height, stem diameter and leaf traits. But, whether these agronomic traits are still have potential selection value in future soybean breeding, we must make comprehensive analysis. For example, short – season cultivars were selected by soybean breeder in Jilin province. This selection was related to demand of farmer, because farmer in Jilin province are accustomed to later sowing and early harvest in soybean production calendar, by this calendar soybean producers are able to adjust labor, this result is consistent with that of Ustun et al [8], but it was different from the result of Morrison et al[14]. Although, the yield did not decrease as shorten of days to maturity, most soybean breeder have believed that days to maturity of soybean cultivars in Jilin province should not shorter than 115 d. Kumudini et al[9] pointed out that yield genetic improvement of short – season soybean was mainly associated with longer leaf area duration and the subsequently greater dry matter accumulation. The correlation of yield and days to maturity is not a true case. In the second example, plant height was decreased with year of release and with the increase of yield, the increase of lodging resistance was related with the decrease of plant height and the increase of stem diameter. But if plant height was further decreased, the number of leaflet and pods would be affected. Voldeng et al[7] pointed out that the reduction in lodging was not achieved through a decrease in plant height. Ustun et al [8] found that plant height decreased until the 1970s, but after that it began to increase in the U. S. Midsouth. The third example was that number of pod and seed were increased with year of release, and were significant positively correlated with yield , but we also found that blighted pod was increased with year of release and increase of yield. This result showed that new cultivars have been well developed in sink capacity, although the ability of source was also been improved, it can not fit the need of sink.

Soybean breeders were mainly focused in agronomic traits, as the limitation of measurement conditions, physiological characteristics were used as selection indexes of high yield had not been put into practical use. So they did not know the changes of physiological characteristics in new released soybean cultivars. Our research showed that genetic improvement of yield and agronomic traits of soybean cultivars has resulted in the improvement of physiological characteristics. Some physiological characteristics, such as photosynthesis, nitrate reductase activity (NRA), volume of nodule, number of nodule and fresh weight of nodule and MDA content were closely correlated with year of release and seed yield of soybean cultivars, but for some physiological characteristics, such as *Pn*, SLW, NRA and MDA content were no greater changes during genetic improvement of 82 years, even they have significant correlation with year of release and yield. For instance, there were significant difference in *Pn* among soybean cultivars [18-23]. Richards [24] pointed out that increase crop photosynthesis might improve yield. Du et al [25] demonstrated that *Pn* among twenty – six soybean cultivars were in the range of 6.9 – 25.2 mol $CO_2 \cdot m^{-2} \cdot s^{-1}$, maximum difference was 18.3 mol$CO_2 \cdot m^{-2} \cdot s^{-1}$. In our results, *Pn* of forty soybean cultivars were in the ranges of 18.6 – 28.3 mol$CO_2 \cdot m^{-2} \cdot s^{-1}$ and most cultivars difference was 9.7 mol$CO_2 \cdot m^{-2} \cdot s^{-1}$ at R2 and R4 stages. But *Pn* has only increased 3.8 molCO_2 $m^{-2} \cdot s^{-1}$ (17.6%) by genetic improvement from 1923 to 2005 according the regression equation. In our recent researches, we found that modern soybean with higher seed yield were mainly correlated with larger leaf area than old soybean cultivars, as the results, modern soybean cultivars had higher photosynthetic ability. Because further increase of plant leaf area or leaf area index would be limited by canopy structure and light transition through canopy, improvement of *Pn* (photosynthetic ability per unit leaf area) would have more potential value in soybean yield genetic improvement[23].

This study demonstrated that soybean breeders have made greater genetic improvement in yield and agronomic traits, at the same time, physiological characteristics have significant changed with year of release and yield. In order to achieve soybean yield breakthrough, it might portend that a new breeding programme of biology and physiological traits as selective indexes must be established in future soybean high yield breeding.

References

[1] Specht J E, Hume D J, Kumudini S V. Soybean yield potential a genetic and physiological perspective[J]. Crop Science, 1999, 39: 1560 – 1570.

[2] Wilcox J R. Sixty years of improvement in publicly developed elite soybean lines[J]. Crop Science, 2001, 41: 1711 – 1716.

[3] Zhao T J, Gai J Y, Li H W, et al. Advances in breeding for super high – yielding soybean cultivars[J]. Scientia Agricultura Sinica, 2006, 39: 29 – 37. (in Chinese with English abstract)

[4] Cox T S, Shroyer J P, Liu B H, et al. Genetic improvement in agronomic traits of hard red winter wheat cultivars from 1919 to 1987 [J]. Crop Science, 1988, 28: 756 – 760.

[5] Luedders V D. Genetic improvement in yield of soybeans[J]. Crop Science, 1977, 17: 971 – 972.

[6] Karmakar P G, Bhatnagar P S. Genetic improvement of soybean varieties released in India from 1969 to 1993[J]. Euphytica, 1996, 90: 95 – 103.

[7] Volgeng H D, Cober E R, Hume D G, et al. Fifty – eight years of genetic improvement of short – season soybean cultivars in Canada [J]. Crop Science, 1997, 37: 428 – 431.

[8] Ustun A, Allen F L, English B C. Genetic progress in soybean of U. S. Midsouth[J]. Crop Science, 2001, 41: 993 – 998.

[9] S, Hume D J, Chu G. Genetic improvement in short season soybeans: 1. Dry matter accumulation, partitioning, and leaf area duration[J]. Crop Science, 2001, 41: 391 – 398.

[10] H B, Xu K Z, Zhao H X, et al. Study on stature evolution of soybean cultivars in Jilin Province[J]. Chinese Journal of Oil Crop Science, 2006, 28: 276 – 281. (in Chinese with English abstract)

[11] Zhao H X, Xu K Z, Yang G Y. et al. Changes and correlations between yield and partial physiological characteristics in leaves of soybean cultivars released from 1923 to 2005 in Jilin Province[J]. Acta Agronomica Sinica, 2008, 34(7): 1259 – 1265. (in Chinese with English abstract)

[12] Jin J, Liu X B, Wang G H. Some eco – physiological characteristic R4 – R5 stage in relation to soybean yield differing in maturities [J]. Scientia Agricultura Sinica, 2004, 37, 1293 – 1300.

[13] Gay S, Egli D B, Reicosky D A. Physiological aspects of yield improvement in soybeans [J]. Agronomy Journal, 1980, 72: 387 – 391.

[14] Morrison M J, Voldeng H D, Cober E R. Physiological changes from 58 years of genetic improvement of short – season soybean cultivars in Canada[J]. Agronomy Journal, 1999, 91: 685 – 689.

[15] Zhu G J, Jiang G M, Hao N B, et al. Relationship between ecophysiological features and grain yield in different soybean varieties[J]. Acta Botanica Sinica, 2002, 44: 725 – 730. (in Chinese with English abstract)

[16] Wang X H, Xu K Z, Zhang Z A, et al. Changes of the protective enzyme activities and lipid peroxidation at seeding stage among soybean varieties cultivated in different stages[J]. Chinese Journal of Oil Crop Science, 2006, 28: 417 – 420. (in Chinese with English abstract)

[17] Boerma H R. Comparison of past and recently developed soybean cultivars in maturity groups VI, VII and VIII[J]. Crop Science, 1979, 19: 611 – 613.

[18] Dornhoff G M, Shibles R M. Varietal difference in net photosynthesis of soybean leaves[J]. Crop Science, 1970, 10: 42 – 45.

[19] Buttery B R, Buzzel R I. Some differences between soybean cultivars observed by growth analysis[J]. Canadian Journal. Plant Science, 1972, 52: 13 – 20.

[20] Ojima M. Improvement of leaf photosynthesis in soybean varieties [J]. Bulletin of the National Institute of Agricultural Sciences of Japan Ser. D, 1972, 23: 97 – 154.

[21] Buttery B R, Buzzell R I, Findlay W I. Relationships among photosynthetic rate, bean yield and other characters in field grown cultivars of soybean[J]. Canadian Jounal of Plant Science, 1981, 61: 191 – 198.

[22] Secor J, McCarty D R, Shibles R, et al. Variability and selection for leaf photosynthesis in advanced generations of soybeans[J]. Crop Science, 1982, 22, 255 – 259.

[23] Ashley D A, Boerma H R. Canopy photosynthesis and its association with seed yield in advanced generations of a soybean cross [J]. Crop Science, 1989, 29: 1042 – 1045.

[24] Richards R A. Selectable traits to increase crop photosynthesis and yield of grain crops[J]. Journal of Expermental Botany, 2000, 51: 447 – 458.

[25] Du W G, Hao N B, Man W Q. High light efficient breeding for soybean[M]. Beijing: Chinese Agricultural Press, 2007: 43 – 105. (in Chinese)